The imagines that have emerged have nearly all been fine and perfect, a very small percentage indeed of deformed insects coming out; and as a rule the house is well adapted, in my opinion, for any exotic species and most of the British, the latter emerging much earlier than would be the case in their wild state; but there is no apparent diminution in size, speaking from imagines obtained from small larvæ, as is frequently the case with larvæ bred in confinement.

June 6, 1881. WM. WATKINS.

The following papers were read :—

1. On the Development of the Skeleton of the Paired Fins of Elasmobranchii, considered in Relation to its Bearings on the Nature of the Limbs of the Vertebrata. By F. M. BALFOUR, F.R.S., F.Z.S., Fellow of Trinity College, Cambridge.

[Received June 2, 1881.]

(Plates LVII., LVIII.)

Some years ago the study of the development of the soft parts of the fins in several Elasmobranch types, more especially in *Torpedo*, led me to the conclusion that the vertebrate limbs were remnants of two continuous lateral fins[1]. More or less similar views (which I was not at that time acquainted with) had been previously held by Maclise, Humphrey, and other anatomists; these views had not, however, met with much acceptance, and diverge in very important points from those put forward by me. Shortly after the appearance of my paper, J. Thacker published two interesting memoirs comparing the skeletal parts of the paired and unpaired fins[2].

In these memoirs Thacker arrives at conclusions as to the nature of the fins in the main similar to mine, but on entirely independent grounds. He attempts to show that the structure of the skeleton of paired fins is essentially the same as that of the unpaired fins, and in this comparison lays special stress on the very simple skeleton of the pelvic fin in the cartilaginous Ganoids, more especially in *Acipenser* and *Polyodon*. He points out that the skeleton of the pelvic fin of *Polyodon* consists essentially of a series of nearly isolated rays, which have a strikingly similar arrangement to that of the rays of the skeleton in many unpaired fins. He sums up his views in the following way[3]:—

[1] Monograph on the Development of Elasmobranch Fishes, pp. 101, 102.

[2] J. K. Thacker, "Median and Paired Fins; a Contribution to the History of the Vertebrate Limbs," Trans. of the Connecticut Acad. vol. iii. 1877.

J. K. Thacker, "Ventral Fins of Ganoids," Trans. of the Connecticut Acad. vol. iv. 1877.

[3] *Loc. cit.* p. 298.

"As the dorsal and anal fins were specializations of the median folds of *Amphioxus*, so the paired fins were specializations of the two lateral folds which are supplementary to the median in completing the circuit of the body. These lateral folds, then, are the homologues of Wolffian ridges, in embryos of higher forms. Here, as in the median fins, there were formed chondroid and finally cartilaginous rods. These became at least twice segmented. The orad ones, with more or less concrescence proximally, were prolonged inwards. The cartilages spreading met in the middle line; and a later extension of the cartilages dorsad completed the limb-girdle.

"The limbs of the Protognathostomi consisted of a series of parallel articulated cartilaginous rays. They may have coalesced somewhat proximally and orad. In the ventral pair they had extended themselves mesiad until they had nearly or quite met and formed the hip-girdle; they had not here extended themselves dorsad. In the pectoral limb the same state of things prevailed, but was carried a step further, namely, by the dorsal extension of the cartilage constituting the scapular portion, thus more nearly forming a ring or girdle."

The most important point in Thacker's theories which I cannot accept is the derivation of the folds, of which the paired fins of the Vertebrata are supposed to be specializations, from the lateral folds of *Amphioxus*; and Thacker himself recognizes that this part of his theory stands on quite a different footing to the remainder.

Not long after the publication of Thacker's paper, an important memoir was published by Mivart in the 'Transactions' of this Society[1]. The object of the researches recorded in this paper was, as Mivart explains, to test how far the hard parts of the limbs and of the azygos fins may have arisen through centripetal chondrifications or calcifications, and so be genetically exoskeletal[2].

Mivart's investigations and the majority of his views were independent of Thacker's memoir; but he acknowledges that he has derived from Thacker the view that pelvic and pectoral girdles, as well as the skeleton of the limbs, may have arisen independently of the axial skeleton.

The descriptive part of Mivart's paper contains an account of the structure of a great variety of interesting and undescribed types of paired and unpaired fins, mainly of Elasmobranchii. The following is the summary given by Mivart of the conclusions at which he has arrived[3]:—

"1. Two continuous lateral longitudinal folds were developed, similar to dorsal and ventral median longitudinal folds.

"2. Separate narrow solid supports (radials), in longitudinal series, and with their long axes directed more or less outwards at right

[1] St. George Mivart, "On the Fins of Elasmobranchii," Zoological Trans. vol. x.

[2] Mivart used the term exoskeletal in an unusual and (as it appears to me) inconvenient manner. The term is usually applied to dermal skeletal structures; but the skeleton of the limbs, with which we are here concerned, is undoubtedly not of this nature.

[3] *Loc. cit.* p. 480.

angles with the long axis of the body, were developed in varying extents in all these four longitudinal folds.

"3. The longitudinal folds became interrupted variously, but so as to form two prominences on each side, *i. e.* the primitive paired limbs.

"4. Each anterior paired limb increased in size more rapidly than the posterior limb.

"5. The bases of the cartilaginous supports coalesced as was needed, according to the respective practical needs of the different separate portions of the longitudinal folds, *i. e.* the respective needs of the several fins.

"6. Occasionally the dorsal radials coalesced (as in *Notidanus* &c.) and sought centripetally (*Pristis* &c.) adherence to the skeletal axis.

"7. The radials of the hinder paired limb did so more constantly, and ultimately prolonged themselves inwards by mesiad growth from their coalesced base, till the piscine pelvic structure arose, as, *e. g.*, in *Squatina*.

"8. The pectoral radials with increasing development also coalesced proximally, and thence prolonging themselves inwards to seek a *point d'appui*, shot dorsad and ventrad to obtain a firm support, and at the same time to avoid the visceral cavity. Thus they came to abut dorsally against the axial skeleton, and to meet ventrally together in the middle line below.

"9. The lateral fins, as they were applied to support the body on the ground, became elongated, segmented, and narrowed, so that probably the line of the propterygium, or possibly that of the mesopterygium, became the cheiropterygial axis.

"10. The distal end of the incipient cheiropterygium either preserved and enlarged preexisting cartilages or developed fresh ones to serve fresh needs, and so grew into the developed cheiropterygium; but there is not yet enough evidence to determine what was the precise course of this transformation.

"11. The pelvic limb acquired a solid connexion with the axial skeleton (a pelvic girdle) through its need of a *point d'appui* as a locomotive organ on land.

"12. The pelvic limb became also elongated; and when its function was quite similar to that of the pectoral limb, its structure became also quite similar (e. g. *Ichthyosaurus, Plesiosaurus, Chelydra*, &c.); but for the ordinary quadrupedal mode of progression it became segmented and inflected in a way generally parallel with, but (from its mode of use) in part inversely to, the inflections of the pectoral limb."

Günther[1] has propounded a theory on the primitive character of the fins, which, on the whole, fits in with the view that the paired fins are structures of the same nature as the unpaired fins. The interest of Günther's views on the nature of the skeleton of the fins more especially depends upon the fact that he attempts to evolve the fin

[1] "Description of *Ceratodus*," Phil. Trans. 1871.

of *Ceratodus* from the typical Selachian type of pectoral fin. His own statement on this subject is as follows[1]:—

"On further inquiry into the more distant relations of the *Ceratodus*-limb, we may perhaps be justified in recognizing in it a modification of the typical form of the Selachian pectoral fin. Leaving aside the usual treble division of the carpal cartilage (which, indeed, is sometimes simple), we find that this shovel-like carpal forms the base for a great number of phalanges, which are arranged in more or less regular transverse rows (zones) and in longitudinal rows (series). The number of phalanges of the zones and series varies according to the species and the form of the fin; in *Cestracion philippi* the greater number of phalanges is found in the proximal zones and middle series, all the phalanges decreasing in size from the base of the fin towards the margins. In a Selachian with a long, pointed, scythe-shaped pectoral fin, like that of *Ceratodus*, we may, from analogy, presume that the arrangement of the cartilages might be somewhat like that shown in the accompanying diagram, which I have divided into nine zones and fifteen series.

"When we now detach the outermost phalanx from each side of the first horizontal zone, and with it the other phalanges of the same series, when we allow the remaining phalanges of this zone to coalesce into one piece (as, in nature, we find coalesced the carpals of *Ceratodus* and many phalanges in Selachian fins), and when we repeat this same process with the following zones and outer series, we arrive at an arrangement identical with what we actually find in *Ceratodus*."

While the researches of Thacker and Mivart are strongly confirmatory of the view at which I had arrived with reference to the nature of the paired fins, other hypotheses as to the nature of the skeleton of the fins have been enunciated, both before and after the publication of my memoir, which are either directly or indirectly opposed to my view.

Huxley in his memoir on *Ceratodus*, which throws light on so many important morphological problems, has dealt with the nature of paired fins[2].

He holds, in accordance with a view previously adopted by Gegenbaur, that the limb of *Ceratodus* "presents us with the nearest known approximation to the fundamental form of vertebrate limb or archipterygium," and is of opinion that in a still more archaic fish than *Ceratodus* the skeleton of the fin "would be made up of homologous segments, which might be termed pteromeres, each of which would consist of a mesomere with a preaxial and a postaxial paramere." He considers that the pectoral fins of Elasmobranchii, more especially the fin of *Notidanus*, which he holds to be the most primitive form of Elasmobranch fin, "results in the simplest possible manner from the shortening of the axis of such a fin-skeleton as that of *Ceratodus*, and the coalescence of some of its elements." Huxley

[1] *Loc. cit.* p. 534.

[2] T. H. Huxley, "On *Ceratodus Fosteri*, with some Observations on the Classification of Fishes," Proc. Zool. Soc. 1876.

does not enter into the question of the origin of the skeleton of the pelvic fin of Elasmobranchii.

It will be seen that Huxley's idea of the primitive structure of the archipterygium is not easily reconcilable with the view that the paired fins are parts of a once continuous lateral fin, in that the skeleton of such a lateral fin, if it has existed, must necessarily have consisted of a series of parallel rays.

Gegenbaur[1] has done more than any other living anatomist to elucidate the nature of the fins; and his views on this subject have undergone considerable changes in the course of his investigations. After Günther had worked out the structure of the fin of *Ceratodus*, Gegenbaur suggested that it constituted the most primitive *persisting* type of fin, and has moreover formed a theory as to the origin of the fins founded on this view, to the effect that the fins, together with their respective girdles, are to be derived from visceral arches with their rays.

His views on this subject are clearly explained in the subjoined passages quoted from the English translation of his 'Elements of Comparative Anatomy,' pp. 473 and 477.

"The skeleton of the free appendage is attached to the extremity of the girdle. When simplest, this is made up of cartilaginous rods (rays), which differ in their size, segmentation, and relation to one another. One of these rays is larger than the rest, and has a number of other rays attached to its sides. I have given the name of *archipterygium* to the ground-form of the skeleton which extends from the limb-bearing girdle into the free appendage. The primary ray is the stem of this archipterygium, the characters of which enable us to follow out the lines of development of the skeleton of the appendage. Cartilaginous arches beset with the rays form the branchial skeleton. The form of skeleton of the appendages may be compared with them; and we are led to the conclusion that it is possible that they may have been derived from such forms. In the branchial skeleton of the Selachii the cartilaginous bars are beset with simple rays. In many a median one is developed to a greater size. As the surrounding rays become smaller, and approach the larger one, we get an intermediate step towards that arrangement in which the larger median ray carries a few smaller ones. This differentiation of one ray, which is thereby raised to a higher grade, may be connected with the primitive form of the appendicular skeleton; and as we compare the girdle with a branchial arch, so we may compare the median ray and its secondary investment of rays with the skeleton of the free appendage.

"All the varied forms which the skeleton of the free appendages

[1] C. Gegenbaur, 'Untersuchungen z. vergleich. Anat. d. Wirbelthiere' (Leipzig, 1864–5): erstes Heft, Carpus u. Tarsus; zweites Heft, Brustflosse d. Fische.
"Ueb. d. Skelet d. Gliedmaassen d. Wirbelthiere im Allgemeinen u. d. Hintergliedmaassen d. Selachier insbesondere," Jenaische Zeitschrift, vol. v. 1870.
"Ueb. d. Archipterygium," Jenaische Zeitschrift, vol vii. 1873.
"Zur Morphologie d. Gliedmaassen d. Wirbelthiere," Morphologisches Jahrbuch, vol. ii. 1876.

exhibits may be derived from a ground-form which persists in a few cases only, and which represents the first, and consequently the lowest, stage of the skeleton in the fin—the *archipterygium*. This is made up of a stem which consists of jointed pieces of cartilage, which is articulated to the shoulder-girdle and is beset on either side with rays which are likewise jointed. In addition to the rays of the stem there are others which are directly attached to the limb-girdle.

"*Ceratodus* has a fin-skeleton of this form; in it there is a stem beset with two rows of rays. But there are no rays in the shoulder-girdle. This biserial investment of rays on the stem of the fin may also undergo various kinds of modifications. Among the Dipnoi, *Protopterus* retains the medial row of rays only, which have the form of fine rods of cartilage; in the Selachii, on the other hand, the lateral rays are considerably developed. The remains of the medial row are ordinarily quite small, but they are always sufficiently distinct to justify us in supposing that in higher forms the two sets of rays might be better developed. Rays are still attached to the stem and are connected with the shoulder-girdle by means of larger plates. The joints of the rays are sometimes broken up into polygonal plates which may further fuse with one another; concrescence of this kind may also affect the pieces which form the base of the fin. By regarding the free rays, which are attached to these basal pieces, as belonging to these basal portions, we are able to divide the entire skeleton of the fin into three segments—pro-, meso-, and metapterygium.

"The metapterygium represents the stem of the archipterygium and the rays on it. The propterygium and the mesopterygium are evidently derived from the rays which still remain attached to the shoulder-girdle."

Since the publication of the memoirs of Thacker, Mivart, and myself a pupil of Gegenbaur's, M. v. Davidoff[1], has made a series of very valuable observations, in part directed towards demonstrating the incorrectness of our theoretical views, more especially Thacker's and Mivart's view of the genesis of the skeleton of the limbs. Gegenbaur[2] has also written a short paper in connexion with Davidoff's memoir, in support of his own as against our views.

It would not be possible here to give an adequate account of Davidoff's observations on the skeleton, muscular system, and nerves of the pelvic fins. His main argument against the view that the paired fins are the remains of a continuous lateral fin is based on the fact that a variable but often considerable number of the spinal nerves in front of the pelvic fin are united by a longitudinal commissure with the true plexus of the nerves supplying the fin. From this he concludes that the pelvic fin has shifted its position, and that it may once therefore have been situated close behind the

[1] M. v. Davidoff, "Beiträge z. vergleich. Anat. d. hinteren Gliedmaassen d. Fische, I.," Morphol. Jahrbuch, vol. v. 1879.

[2] "Zur Gleidmaassenfrage. An die Untersuchungen von Davidoff's angeknüpfte Bemerkungen," Morphol. Jahrbuch, vol. v. 1879.

visceral arches. Granting, however, that Davidoff's deduction from the character of the pelvic plexus is correct, there is, so far as I see, no reason in the nature of the lateral-fin theory why the pelvic fins should not have shifted; and, on the other hand, the longitudinal cord connecting some of the ventral roots in front of the pelvic fin may have another explanation. It may, for instance, be a remnant of the time when the pelvic fin had a more elongated form than at present, and accordingly extended further forwards.

In any case our knowledge of the nature and origin of nervous plexuses is far too imperfect to found upon their characters such conclusions as those of Davidoff.

Gegenbaur, in his paper above quoted, further urges against Thacker and Mivart's views the fact that there is no proof that the fin of *Polyodon* is a primitive type; and also suggests that the epithelial line which I have found connecting the embryonic pelvic and pectoral fins in *Torpedo* may be a rudiment indicating a migration backwards of the pelvic fin.

With reference to the development of the pectoral fin in the Teleostei there are some observations of 'Swirski[1], which unfortunately do not throw very much light upon the nature of the limb.

'Swirski finds that in the Pike the skeleton of the limb is formed of a plate of cartilage continuous with the pectoral girdle, which soon becomes divided into a proximal and a distal portion. The former is subsequently segmented into five basal rays, and the latter into twelve parts, the number of which subsequently becomes reduced.

The observations which I have to lay before the Society were made with the object of determining how far the development of the skeleton of the limbs throws light on the points on which the anatomists whose opinions have just been quoted are at variance.

They were made, in the first instance, to complete a chapter in my work on comparative embryology; and, partly owing to the press of other engagements, but still more to the difficulty of procuring material, my observations are confined to the two British species of the genus *Scyllium*, viz. *Sc. stellare* and *Sc. canicula*; yet I venture to believe that the results at which I have arrived are not wholly without interest.

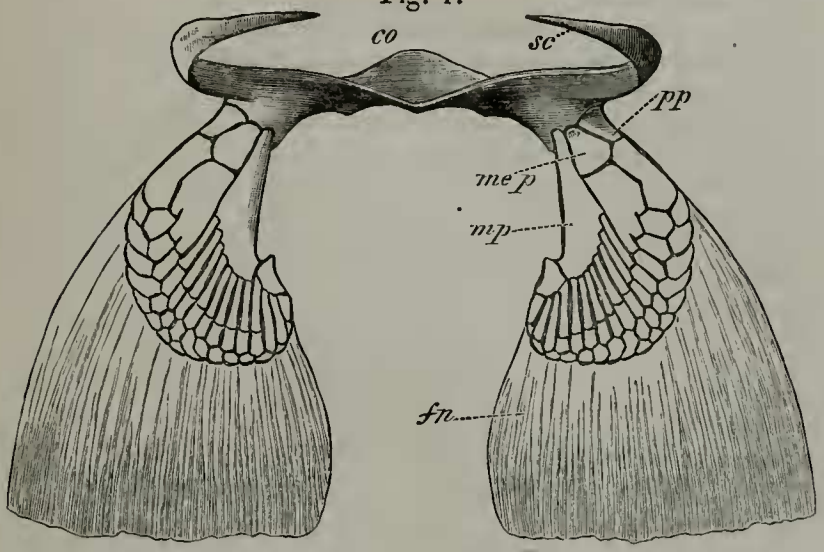
Before dealing with the development of the skeleton of the fin, it will be convenient to describe with great brevity the structure of the pectoral and pelvic fins of the adult. The pectoral fins consist of broad plates inserted horizontally on the sides of the body; so that in each there may be distinguished a dorsal and a ventral surface, and an anterior and a posterior border. Their shape may best be gathered from the woodcut (fig. 1); and it is to be especially noted that the narrowest part of the fin is the base, where it is attached to the side of the body. The cartilaginous skeleton only occupies

[1] G. 'Swirski, 'Untersuch. üb. d. Entwick. d. Schultergürtels u. d. Skelets d. Brustflosse d. Hechts.' Inaug. Diss. Dorpat, 1880.

a small zone at the base of the fin, the remainder being formed of a fringe supported by radiately arranged horny fibres[1].

The true skeleton consists of three basal pieces articulating with the pectoral girdle; on the outer side of which there is a series of more

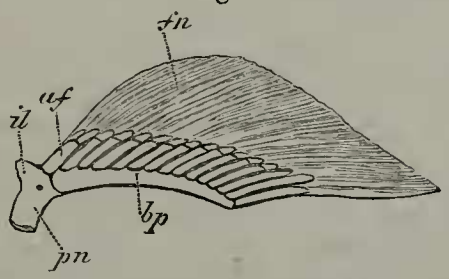
Fig. 1.



Pectoral fins and girdle of an adult of *Scyllium canicula* (natural size, seen from behind and above.)

co. Coracoid; *sc.* scapula; *pp.* propterygium; *mcp.* mesopterygium; *mp.* metapterygium; *fn.* part of fin supported by horny fibre.

Fig. 2.



Right pelvic fin and part of pelvic girdle of an adult female of *Scyllium canicula* (natural size).

il. iliac process; *pn.* pubic process, cut across below; *bp.* basipterygium; *af.* anterior cartilaginous fin-ray articulated to pelvic girdle; *fn.* part of fin supported by horny fibres.

or less segmented cartilaginous fin-rays. Of the basal cartilages one (*pp*) is anterior, a second (*mep*) is placed in the middle, and a third is posterior (*mp*). They have been named by Gegenbaur the *pro-*

[1] The horny fibres are mesoblastic products; they are formed, in the first instance, as extremely delicate fibrils on the inner side of the membrane separating the epiblast from the mesoblast.

pterygium, the *mesopterygium*, and the *metapterygium*; and these names are now generally adopted.

The metapterygium is by far the most important of the three, and in *Scyllium canicula* supports 12 or 13 rays[1]. It forms a large part of the posterior boundary of the fin, and bears rays only on its *anterior* border.

The mesopterygium supports 2 or 3 rays, in the basal parts of which the segmentation into distinct rays is imperfect; and the propterygium supports only a single ray.

The pelvic fins are horizontally placed, like the pectoral fins, but differ from the latter in nearly meeting each other along the median ventral line of the body. They also differ from the pectoral fins in having a relatively much broader base of attachment to the sides of the body. Their cartilaginous skeleton (woodcut, fig. 2) consists of a basal bar, placed parallel to the base of the fin, and articulated in front with the pelvic girdle.

On its outer border it articulates with a series of cartilaginous fin-rays. I shall call the basal bar the basipterygium. The rays which it bears are most of them less segmented than those of the pectoral fin, being only divided into two; and the posterior ray, which is placed in the free posterior border of the fin, continues the axis of the basipterygium. In the male it is modified in connexion with the so-called clasper.

The anterior fin-ray of the pelvic fin, which is broader than the other rays, articulates directly with the pelvic girdle, instead of with the basipterygium. This ray, in the female of *Scyllium canicula* and in the male of *Scyllium catulus* (Gegenbaur), is peculiar in the fact that its distal segment is longitudinally divided into two or more pieces, instead of being single as is the case with the remaining rays. It is probably equivalent to two of the posterior rays.

Development of the paired Fins.—The first rudiments of the limbs appear in *Scyllium*, as in other fishes, as slight longitudinal ridge-like thickenings of the epiblast, which closely resemble the first rudiments of the unpaired fins.

These ridges are two in number on each side—an anterior immediately behind the last visceral fold, and a posterior on the level of the cloaca. In most Fishes they are in no way connected; but in some Elasmobranch embryos, more especially in that of *Torpedo*, they are connected together at their first development by a line of columnar-epiblast cells. This connecting line of columnar epiblast, however, is a very transitory structure. The rudimentary fins soon become more prominent, consisting of a projecting ridge both of epiblast and mesoblast, at the outer edge of which is a fold of epiblast only, which soon reaches considerable dimensions. At a later stage the mesoblast penetrates into this fold, and the fin becomes a simple ridge of mesoblast covered by epiblast. The pectoral fins are at first considerably ahead of the pelvic fins in development.

The direction of the original epithelial line which connected the

[1] In one example where the metapterygium had 13 rays the mesopterygium had only 2 rays.

two fins of each side is nearly, though not quite, longitudinal, sloping somewhat obliquely ventralwards. It thus comes about that the attachment of each pair of limbs is somewhat on a slant, and that the pelvic pair nearly meet each other in the median ventral line shortly behind the anus.

The embryonic muscle-plates, as I have elsewhere shown, grow into the bases of the fins; and the cells derived from these ingrowths, which are placed on the dorsal and ventral surfaces in immediate contact with the epiblast, probably give rise to the dorsal and ventral muscular layers of the limb, which are shown in section in Plate LVII. fig. 1 *m* and in Plate LVIII. fig. 7 *m*.

The cartilaginous skeleton of the limbs is developed in the indifferent mesoblast cell between the two layers of muscles. Its early development in both the pectoral and the pelvic fins is very similar. When first visible it differs histologically from the adjacent mesoblast simply in the fact of its cells being more concentrated; while its boundary is not sharply marked.

At this stage it can only be studied by means of sections. It arises simultaneously and continuously with the pectoral and pelvic girdles, and consists, in both fins, of a bar springing at right angles from the posterior side of the pectoral or pelvic girdle, and running parallel to the long axis of the body along the base of the fin. The outer side of this bar is continued into a thin plate, which extends into the fin.

The structure of the skeleton of the fin slightly after its first differentiation will be best understood from Plate LVII. fig. 1, and Plate LVIII. fig. 7. These figures represent transverse sections through the pelvic and pectoral fins of the same embryo on the same scale. The basal bar is seen at *bp*, and the plate at this stage (which is considerably later than the first differentiation) already partially segmented into rays at *br*. Outside the region of the cartilaginous plate is seen the fringe with the horny fibres (*h.f*); and dorsally and ventrally to the cartilaginous skeleton are seen the already well-differentiated muscles (*m*).

The pectoral fin is shown in horizontal section in Plate LVIII. fig. 6, at a somewhat earlier stage than that to which the transverse sections belong. The pectoral girdle (*p.g*) is cut transversely, and is seen to be perfectly continuous with the basal bar (*bp*) of the fin. A similar continuity between the basal bar of the pelvic fin and the pelvic girdle is shown in Plate LVII. fig. 2, at a somewhat later stage. The plate continuous with the basal bar of the fin is at first, to a considerable extent in the pectoral, and to some extent in the pelvic fin, a continuous lamina, which subsequently segments into rays. In the parts of the plate which eventually form distinct rays, however, almost from the first the cells are more concentrated than in those parts which will form the tissue between the rays; and I am not inclined to lay any stress whatever upon the fact of the cartilaginous fin-rays being primitively part of a continuous lamina, but regard it as a secondary phenomenon, dependent on the mode of conversion of embryonic mesoblast cells into cartilage. In all cases the separation

into distinct rays is to a large extent completed before the tissue of which the plates are formed is sufficiently differentiated to be called cartilage by an histologist.

The general position of the fins in relation to the body, and their relative sizes, may be gathered from Plate LVII. figs. 4 and 5, which represent transverse sections of the same embryo as that from which the transverse sections showing the fin on a larger scale were taken.

During the first stage of its development the skeleton of both fins may thus be described as consisting of *a longitudinal bar running along the base of the fin, and giving off at right angles series of rays which pass into the fin*. The longitudinal bar may be called the basipterygium; and it is continuous in front with the pectoral or pelvic girdle, as the case may be.

The further development of the primitive skeleton is different in the case of the two fins.

The Pelvic Fin.—The changes in the pelvic fin are comparatively slight. Plate LVII. fig. 2 is a representation of the fin and its skeleton in a female of *Scyllium stellare* shortly after the primitive tissue is converted into cartilage, but while it is still so soft as to require the very greatest care in dissection. The fin itself forms a simple projection of the side of the body. The skeleton consists of a basipterygium (*bp*), continuous in front with the pelvic girdle. To the outer side of the basipterygium a series of cartilaginous fin-rays are attached—the posterior ray forming a direct prolongation of the basipterygium, while the anterior ray is united rather with the pelvic girdle than with the basipterygium. All the cartilaginous fin-rays except the first are completely continuous with the basipterygium, their structure in section being hardly different from that shown in Plate LVII. fig. 1.

The external form of the fin does not change very greatly in the course of the further development; but the hinder part of the attached border is, to some extent, separated off from the wall of the body, and becomes the posterior border of the adult fin. With the exception of a certain amount of segmentation in the rays, the character of the skeleton remains almost as in the embryo. The changes which take place are illustrated by Plate LVII. fig. 3, showing the fin of a young male of *Scyllium stellare*. The basipterygium has become somewhat thicker, but is still continuous in front with the pelvic girdle, and otherwise retains its earlier characters. The cartilaginous fin-rays have now become segmented off from it and from the pelvic girdle, the posterior end of the basipterygial bar being segmented off as the terminal ray.

The anterior ray is directly articulated with the pelvic girdle, and the remaining rays continue articulated with the basipterygium. Some of the latter are partially segmented.

As may be gathered by comparing the figure of the fin at the stage just described with that of the adult fin (woodcut, fig. 2), the remaining changes are very slight. The most important is the segmentation of the basipterygial bar from the pelvic girdle.

The pelvic fin thus retains in all essential points its primitive structure.

The Pectoral Fin.—The earliest stage of the pectoral fin differs, as I have shown, from that of the pelvic fin only in minor points (Plate LVIII. fig. 6). There is the same longitudinal or basipterygial bar (*bp*), to which the fin-rays are attached, which is continuous in front with the pectoral girdle (*p g*). The changes which take place in the course of the further development, however, are very much more considerable in the case of the pectoral than in that of the pelvic fin.

The most important change in the external form of the fin is caused by a reduction in the length of its attachment to the body. At first (Plate LVIII. fig. 6), the base of the fin is as long as the greatest breadth of the fin; but it gradually becomes shortened by being constricted off from the body at its hinder end. In connexion with this process the posterior end of the basipterygial bar is gradually rotated outwards, its anterior end remaining attached to the pectoral girdle. In this way this bar comes to form the posterior border of the skeleton of the fin (Plate LVIII. figs. 8 & 9), constituting the metapterygium (*mp*). It becomes eventually segmented off from the pectoral girdle, simply articulating with its hinder edge.

The plate of cartilage, which is continued outwards from the basipterygium, or, as we may now call it, the metapterygium, into the fin, is not nearly so completely divided up into fin-rays as the homologous part of the pelvic fin; and this is especially the case with the basal part of the plate. This basal part becomes, in fact, at first only divided into two parts (Plate LVIII. fig. 8)—a small anterior part at the front end (*me.p*), and a larger posterior along the base of the metapterygium (*mp*); and these two parts are not completely segmented from each other. The anterior part directly joins the pectoral girdle at its base, resembling in this respect the anterior fin-ray of the pelvic girdle. It constitutes the (at this stage undivided) rudiment of the mesopterygium and propterygium of Gegenbaur. It bears in my specimen of this age four fin-rays at its extremity, the anterior not being well marked. The remaining fin-rays are prolongations outwards of the edge of the plate continuous with the metapterygium. These rays are at the stage figured more or less transversely segmented; but at their outer edge they are united together by a nearly continuous rim of cartilage. The spaces between the fin-rays are relatively considerably larger than in the adult.

The further changes in the cartilages of the pectoral limb are, morphologically speaking, not important, and are easily understood by reference to Plate LVIII. fig. 9 (representing the skeleton of the limb of a nearly ripe embryo). The front end of the anterior basal cartilage becomes segmented off as a propterygium (*pp*), bearing a single fin-ray, leaving the remainder of the cartilage as a mesopterygium (*mes*). The remainder of the now considerably segmented fin-rays are borne by the metapterygium.

General Conclusions.—From the above observations, conclusions of a positive kind may be drawn as to the primitive structure of the

skeleton; and the observations have also, it appears to me, important bearings on the theories of my predecessors in this line of investigation.

The most obvious of the positive conclusions is to the effect that the embryonic skeleton of the paired fins consists of a series of parallel rays similar to those of the unpaired fins. These rays support the soft parts of the fins, which have the form of a longitudinal ridge; and they are continuous at their base with a longitudinal bar. This bar, from its position at the base of the fin, can clearly never have been a median axis with the rays on both sides. It becomes the basipterygium in the pelvic fin, which retains its embryonic structure much more completely than the pectoral fin; and the metapterygium in the pectoral fin. The metapterygium of the pectoral fin is thus clearly homologous with the basipterygium of the pelvic fin, as originally supposed by Gegenbaur, and as has since been maintained by Mivart. The propterygium and mesopterygium are obviously relatively *unimportant* parts of the skeleton as compared with the metapterygium.

My observations on the development of the skeleton of the fins certainly do not of themselves demonstrate that the paired fins are remnants of a once continuous lateral fin; but they support this view in that they show the primitive skeleton of the fins to have exactly the character which might have been anticipated if the paired fins had originated from a continuous lateral fin. The longitudinal bar of the paired fins is believed by both Thacker and Mivart to be due to the coalescence of the bases of the primitively independent rays of which they believe the fin to have been originally composed. This view is probable enough in itself, and is rendered more so by the fact, pointed out by Mivart, that a longitudinal bar supporting the cartilaginous rays of unpaired fins is occasionally formed; but there is no trace in the embryo Scylliums of the bar in question being formed by the coalescence of rays, though the fact of its being perfectly continuous with the bases of the fin-rays is somewhat in favour of such coalescence.

Thacker and Mivart both hold that the pectoral and pelvic girdles are developed by ventral and dorsal growths of the anterior end of the longitudinal bar supporting the fin-rays.

There is, so far as I see, no theoretical objection to be taken to this view; and the fact of the pectoral and pelvic girdles originating continuously and long remaining united with the longitudinal bars of their respective fins is in favour of it rather than the reverse. The same may be said of the fact that the first part of each girdle to be formed is that in the neighbourhood of the longitudinal bar (basipterygium) of the fin, the dorsal and ventral prolongations being subsequent growths.

On the whole my observations do not throw much light on the theories of Thacker and Mivart as to the genesis of the skeleton of the paired fin; but, so far as they bear on the subject, they are distinctly favourable to those theories.

The main results of my observations appear to me to be decidedly adverse to the views recently put forward on the structure of the fin

by Gegenbaur and Huxley, both of whom, as stated above, consider the primitive type of fin to be most nearly retained in *Ceratodus*, and to consist of a central multisegmented axis with numerous lateral rays.

Gegenbaur derives the Elasmobranch pectoral fin from a form which he calls the archipterygium, nearly like that of *Ceratodus*, with a median axis and two rows of rays—but holds that in addition to the rays attached to the median axis, which are alone found in *Ceratodus*, there were other rays directly articulated to the shoulder-girdle. He considers that in the Elasmobranch fin the majority of the lateral rays on the posterior (or median according to his view of the position of the limb) side have become aborted, and that the central axis is represented by the metapterygium; while the pro- and mesopterygium and their rays are, he believes, derived from those rays of the archipterygium which originally articulated directly with the shoulder-girdle.

This view appears to me to be absolutely negatived by the facts of development of the pectoral fin in *Scyllium*—not so much because the pectoral fin in this form is necessarily to be regarded as primitive, but because what Gegenbaur holds to be the primitive axis of the biserial fin is demonstrated to be really the base, and it is only in the adult that it is conceivable that a second set of lateral rays could have existed on the posterior side of the metapterygium. If Gegenbaur's view were correct, we should expect to find in the embryo, if anywhere, traces of the second set of lateral rays; but the fact is that, as may easily be seen by an inspection of figs. 6 and 7, such a second set of lateral rays could not possibly have existed in a type of fin like that found in the embryo. With this view of Gegenbaur's it appears to me that the theory held by this anatomist to the effect that the limbs are modified gill-arches also falls, in that his method of deriving the limbs from gill-arches ceases to be admissible, while it is not easy to see how a limb, formed on the type of the embryonic limb of Elasmobranchs, could be derived from a gill-arch with its branchial rays.

Gegenbaur's older view, that the Elasmobranch fin retains a primitive uniserial type, appears to me to be nearer the truth than his more recent view on this subject; though I hold the fundamental point established by the development of these parts in *Scyllium* to be that the posterior border of the adult Elasmobranch pectoral fin is the primitive base-line, *i.e.* line of attachment of the fin to the side of the body.

Huxley holds that the mesopterygium is the proximal piece of the axial skeleton of the limb of *Ceratodus*, and derives the Elasmobranch fin from that of *Ceratodus* by the shortening of its axis and the coalescence of some of its elements. The entirely secondary character of the mesopterygium, and its total absence in the young embryo *Scyllium*, appear to me as conclusive against Huxley's view as the character of the embryonic fin is against that of Gegenbaur; and I should be much more inclined to hold that the fin of *Ceratodus* has been derived from a fin like that of the Elasmobranchs by a series of steps similar to those which Huxley supposes to have led

to the establishment of the Elasmobranch fin, but in exactly the reverse order.

There is one statement of Davidoff's which I cannot allow to pass without challenge. In comparing the skeletons of the paired and unpaired fins he is anxious to prove that the former are independent of the axial skeleton in their origin and that the latter have been segmented from the axial skeleton, and thus to show that an homology between the two is impossible. In support of his view he states[1] that he has satisfied himself, from embryos of *Acanthias* and *Scyllium*, that the rays of the unpaired fins *are undoubtedly products of the segmentation of the dorsal and ventral spinous processes.*

This statement is wholly unintelligible to me. From my examination of the development of the first dorsal and the anal fins of *Scyllium* I find that their rays develop at a considerable distance from, and quite independently of, the neural and hæmal arches, and that they are at an early stage of development distinctly in a more advanced state of histological differentiation than the neural and hæmal arches of the same region. I have also found exactly the same in the embryos of *Lepidosteus*.

I have, in fact, no doubt that the skeleton of both the paired and the unpaired fins of Elasmobranchs and *Lepidosteus* is in its development independent of the axial skeleton. The phylogenetic mode of origin of the skeleton both of the paired and of the unpaired fins cannot, however, be made out without further investigation.

EXPLANATION OF THE PLATES.

Plate LVII.

Fig. 1. Transverse section through the pelvic fin of an embryo of *Scyllium* belonging to stage P[2], magnified 50 diameters. *bp*, basipterygium; *br*, fin ray; *m*, muscle; *hf*, horny fibres supporting the peripheral part of the fin.

2. Pelvic fin of a very young female embryo of *Scyllium stellare*, magnified 16 diameters. *bp*, basipterygium; *pu*, pubic process of pelvic girdle (cut across below); *il*, iliac process of pelvic girdle; *fo*, foramen.

3. Pelvic fin of a young male embryo of *Scyllium stellare*, magnified 16 diameters. *bp*, basipterygium; *mo*, process of basipterygium continued into clasper: *il*, iliac process of pelvic girdle; *pu*, pubic section of pelvic girdle.

4. Transverse section through the ventral part of the trunk of an embryo *Scyllium* of stage P, in the region of the pectoral fins, to show how the fins are attached to the body, magnified 18 diameters. *br*, cartilaginous fin-ray; *bp*, basipterygium; *m*, muscle of fin; *mp*, muscle-plate.

5. Transverse section through the ventral part of the trunk of an embryo *Scyllium* of stage P, in the region of the pelvic fin, on the same scale as fig. 4. *bp*, basipterygium; *br*, cartilaginous fin-rays; *m*, muscle of the fins; *mp*, muscle-plate.

Plate LVIII.

Fig. 6. Pectoral fin of an embryo of *Scyllium canicula*, of a stage between O

[1] Loc. cit. p. 514.

[2] I employ here the same letters to indicate the stages as in my Monograph on Elasmobranch Fishes.